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Review article

Bioprotective yeasts: Potential to limit postharvest spoilage and to extend shelf life or improve microbial safety of processed foods

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ABSTRACT

Yeasts are a widespread group of microorganisms that are receiving increasing attention from scientists and industry. Their diverse biological activities and broad-spectrum antifungal activity make them promising candidates for application, especially in postharvest biocontrol of fruits and vegetables and food biopreservation. The present review focuses on recent knowledge of the mechanisms by which yeasts inhibit pathogenic fungi and/or spoilage fungi and bacteria. The main mechanisms of action of bioprotective yeasts include competition for nutrients and space, synthesis and secretion of antibacterial compounds, mycoparasitism and the secretion of lytic enzymes, biofilm formation, quorum sensing, induced systemic resistance of fruit host, as well as the production of reactive oxygen species. Preadaptation of yeasts to abiotic stresses such as cold acclimatization and sublethal oxidative stress can improve the effectiveness of antagonistic yeasts and thus more effectively play biocontrol roles under a wider range of environmental conditions, thereby reducing economic losses. Combined application with other antimicrobial substances can effectively improve the efficacy of yeasts as biocontrol agents. Yeasts show great potential as substitute for chemical additives in various food fields, but their commercialization is still limited. Hence, additional investigation is required to explore the prospective advancements of yeasts in the field of biopreservation for food.

1. Introduction

The confluence of postharvest decay, attributed to fungal pathogens, along with the presence of pathogenic and food-spoiling bacteria, represents a formidable obstacle in the realm of global food security [1,2]. The use of synthetic fungicides remains the predominant strategy to control postharvest microbial spoilage [3]. However, their use is being increasingly questioned due to environmental and food safety concerns, highlighting the need for alternative management strategies. In this context, the utilization of wild species and strains of antagonistic yeast species presents a promising option to minimize postharvest losses, offering a sustainable and safe solution for the increasing worldwide demand for food [4,5]. Yeasts are ubiquitous microorganisms found in diverse environments, such as terrestrial, aquatic, and aerial habitats. They have been utilized in various fields, including agriculture, biotechnology, food industry, veterinary medicine, environmental protection, and medical applications. One of the key advantages of yeasts is their potent antifungal and antagonistic activities, making them ideal candidates for controlling fungal pathogens. Additionally, their ability to grow under various conditions, exhibit stress resistance, and ease of cultivation have further increased their significance in diverse applications [6–9]. More recently, some yeasts have been delineated as efficacious antagonists against a diverse array of plant

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pathogens, particularly recommended for the prevention and control of pre- and post-harvest diseases afflicting fruits and vegetables attributable to mold proliferation.

Yeasts are attractive candidates for biological control due to their broad-spectrum antimicrobial activity, genetic stability, low nutritional requirements, and ability to thrive at low temperatures. Furthermore, yeasts can withstand adverse pH and oxidative stress conditions. These properties support the possibility of using yeast as a biological antagonist. In recent years, several antagonistic yeasts belonging to the genera *Pichia* [10], *Rhodosporidium* [11], *Debaryomyces* [12], *Candida* [13], *Metschnikowia* [14], *Pseudozyma* [15], and *Hanseniaspora* [16] have been utilized as effective biological control agents against postharvest diseases in fruits and vegetables. Understanding the mechanisms of yeast antagonistic properties paves the way for the development of more sustainable and efficient post-harvest biocontrol with deeper indispensable.

Fungal genera like *Aspergillus*, *Penicillium*, *Alternaria*, and *Fusarium* contribute to postharvest spoilage and reduce the quality of processed foods. These fungi produce mycotoxins, which are toxic secondary metabolites that can withstand various food processing steps and pose a significant threat to human and animal health [17]. The economic losses resulting from these food safety concerns affect both producers and consumers and highlight the need for effective management strategies. The process of utilizing natural or added microorganisms, or their metabolites to increase the safety and extend the shelf-life of food is known as biopreservation, biocontrol and biological control [18]. This involves using microorganisms to prevent the growth of spoilage or pathogenic microorganisms. Yeasts has been proposed based on its GRAS status granted by the Food and Drug Administration (FDA). Certain yeast types are recommended in the list of qualified presumption of safety (QSP) for intentional addition to food or feed notified by the European Food Safety Authority (EFSA) [19]. While the antagonistic activity of yeasts has been extensively researched and utilized in the biological control of postharvest diseases in fruits and the management of unwanted yeasts in the brewing and wine industries, there is relatively little research on using yeasts as biocontrol agents in processed foods such as coffee, juices, cheese, dry-cured meat products, and fermented products. This represents a potential area for further investigation and development in the field of biopreservation [20, 21].

The current review provides a concise summary of the research that has contributed to a better understanding of postharvest biocontrol systems. Several yeast genera that have demonstrated promising results are highlighted. This review also outlines the mechanisms by which yeasts can antagonize pathogenic and spoilage fungi and bacteria, as well as strategies to enhance the performance and effectiveness of yeasts as biocontrol agents. Finally, some information on the good application of yeasts in processed foods is provided.

2. Biocontrol of yeasts in agricultural products

There have been numerous reports on the applications of antagonistic yeasts in postharvest biological control of various fruits including apple [22], pear [23], banana [24], kiwifruit [25], citrus [14], grape [26], papaya [27], as well as strawberry [28], and pineapple [29]. Additionally, the use of antagonist yeasts for the biocontrol of vegetables such as potatoes [30], tomatoes [31] and chilies [32] has been extensively documented. Moreover, antagonist yeasts have also been employed in controlling mold in grains,

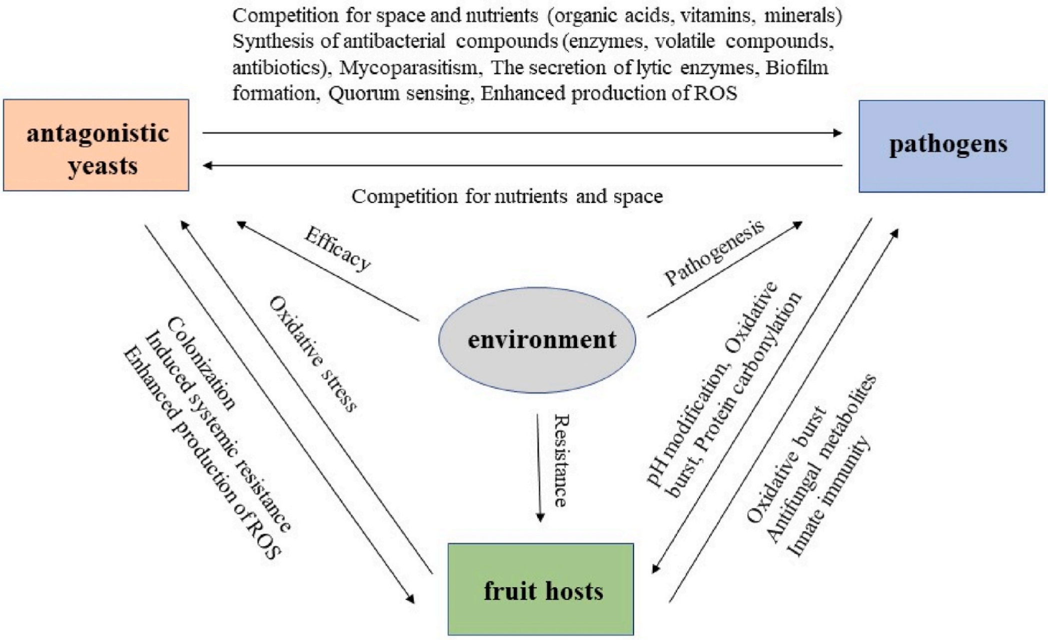

Fig. 1. Diagram of potential interactions between the fruit hosts, pathogens, and antagonistic yeasts within their respective environments.

which are prone to mycotoxin contamination [33].

The postharvest biological control system is a complex network comprising of antagonistic yeasts, pathogens, and fruit hosts, and their interactions with environmental constraints must be considered (Fig. 1). These complex interactions are key factors in determining the success of biocontrol strategies for postharvest diseases. Effective postharvest biocontrol relies on selecting appropriate microbial antagonists, understanding the mechanisms underlying their interactions with pathogens and hosts, and optimizing environmental conditions to promote their efficacy. In this context, Kusstatscher et al. [34] proposed that microbiome approaches will provide the key to biologically control postharvest pathogens and storability of fruits and vegetables, based on the observations that (i) high-throughput sequencing-based techniques including advanced microscopy reveal fruits and vegetables as holobionts and (ii) that the indigenous microbiome of fruits and vegetables is affected by field and postharvest handling which influence the storability of fruits and vegetables. Ongoing research efforts are thus focused on improving our understanding of the factors that influence these interactions, with the ultimate goal of developing more sustainable and efficient postharvest biocontrol strategies.

The antagonistic activity of yeasts against deleterious microorganisms encompasses processes of spatial and oxygenic competition, as well as the synthesis and exudation of antifungal secondary metabolites, including toxins, enzymes, and volatile compounds [35]. Additionally, it entails the elicitation of systemic resistance within host plant organisms [36]. In addition, numerous studies have demonstrated that some yeast strains possess detoxification functions, converting toxins produced by fungi into non-toxic or low-toxic substances to defend against fungal attack [37]. Various attempts have been made to improve the effectiveness of antagonistic yeasts against harmful microorganisms by increasing their viability or by combining them with other physical or chemical means. In this section of the review, yeasts from different yeast genera as biocontrol agents are listed to provide a more comprehensive understanding of postharvest biocontrol systems. Additionally, we discuss the mechanisms by which these yeasts could inhibit the growth of pathogenic and spoilage microorganisms, thereby highlighting their potential as protective agents for processed foods. Table 1 lists the antagonistic yeasts that have been extensively investigated in recent years for their use in postharvest disease management.

2.1. Antagonistic yeasts

2.1.1. 1. Candida spp.

The genus *Candida* is routinely recovered from environmental samples. Interestingly many *Candida* isolates strongly inhibit plant pathogens. Representatives are, for example, *Candida sake* CPA-1 [67], *Candida pseudolambica* W16 [13], *Candida albicans* [68,69], *Candida oleophila* [70], *Candida pyralidae* Y63 [71], *Candida tropicalis* [72], *Candida subhashii* [73], which are envisaged as biological

Table 1
Antagonistic yeasts used for post-harvest disease management.

Yeast Genera	Species	Pathogen	Host fruit	Reference
Candida	*C. membranifaciens*	*B. cinerea*	Grape	[38]
	C. oleophila	*B. cinerea* and *Alternaria alternata*	Kiwifruit	[39]
	C.sake 41E	*P. expansum*	Apple	[40]
	C. orthopsilosis	*A. flavus* and *Aspergillus niger*	Citrus	[41]
Pichia	*P. kudriavzevii*	*P. glabrum*	Grape	[42]
	P. guilliermondii	*R. stolonifera,* and *P. expansum*	Peach	[43]
	P. kudriavzeviii CMIAT171	*Lasiodiplodia theobromae* and *Neofusicoccum parvum*	Mango	[44]
	P. galeiformis (BAF03)	*P. digitatum*	Citrus	[45]
	P. anomala Kh6	*B. cinerea*	Apple	[46]
Metschnikowia	*M. pulcherrima*	*B. cinerea*	Apple	[47]
	M. guilliermondii	*B. cinerea*	Grape	[38]
	M. guilliermondii	green and blue molds	Citrus	[48]
	M. pulcherrima GP8	*B. cinerea*	Grape	[49]
	M. aff. Fructicola	*Penicillium*	Lemon	[50]
	M. caribbica	*C. gloeosporioides*	Mango	[51]
Debaryomyces	*D. hansenii*	*Penicillium citrinum*	Persian lime	[52]
	Debaryomyces nepalensis	*C. gloeosporioides*	Mango	[53]
	D. hansenii F9D	*P. expansum*	Apple and pear	[54]
	D. hansenii	*B. cinerea* and *A. alternata*	Kiwifruit	[55]
Hanseniaspora	*H. osmophila*	*B. cinerea*	Grape	[56]
	H. guilliermondii YBB3	*Aspergillus* spp.	Grape	[57]
	H. uvarum and *H. clermontiae*	*B. cinerea*	Grape	[58]
	H. opuntiae (CCMA 0760)	*B. cinerea*	Grape	[59]
Cryptococcus	*C. podzolicus*	blue mold	Pear	[60]
	C. podzolicus	*P. expansum*	Apple	[61]
	C. laurentii	*B. cinerea*	Cherry and tomato	[62]
	C. laurentii	*P. italicum*	Citrus	[63]
Aureobasidium	*A. pullulans*	*A. flavus* and *A. niger*	Citrus	[41]
		B. cinerea	Grape	[56]
Kluyveromyces	*K. marxianus*	gray mold	strawberry	[64]
Rhodotorula	*R. mucilaginosa*	*P. expansum* and *R. stolonifera*	Peach	[65]
Sporidiobolus	*S. pararoseus* Y16	*A. niger*	Grape	[66]
Wickerhamomyces	*W. anomalus*	*B. cinerea*	Tomato	[31]

control agents to control mold and postharvest diseases in pome, stone fruits as well as citrus fruits. Its antagonistic effect has been tested to be effective in most fruits, including apple [74], mango [75], orange [41], grape [76], banana [77], tomato [78], citrus [79], litchi [80], peach [13], etc. One study showed that *C. sake* was effective in controlling *Penicillium digitatum*, a common post-harvest pathogen in pome fruits [40]. Another study found that *C. oleophila*, when applied as a post-harvest treatment on grape, elicited systemic resistance against *P. digitatum*, the main postharvest pathogen of citrus fruit [81].

Demonstrating its efficacy as a biocontrol agent, *Candida* exhibited enhanced colonization in wounded fruit tissues, particularly when treated with caffeic acid, resulting in superior biocontrol performance against gray and blue mold in kiwifruit. This aligns with previous findings on the biocontrol capabilities of *C. oleophila*, underscoring the significance of its population dynamics and stress tolerance, notably observed within the initial 48 h, in contributing to effective postharvest disease management [82,83]. Nonetheless, certain challenges associated with the use of *Candida* as a biocontrol agent for post-harvest disease management remain, such as variation in effectiveness dependent on the species and strain employed, the inoculum concentration, and environmental conditions.

2.1.2. *Pichia spp.*

Several species within the *Pichia* genus, such as *Pichia guilliermondii* [84], *Pichia caribbica* [85], *Pichia membranifaciens* NPCC 1250 [86], *Penicillium italicum* [87], *Pichia anomala* [46], have been identified as effective biocontrol agents against various postharvest pathogens. These pathogens include *Colletotrichum acutatum, Penicillium glabrum, Penicillium expansum, P. digitatum, Botrytis cinerea, Alternaria solani* and *Rhizopus stolonifer*, on a variety of fruits [42,45,87]. In particular, *Pichia* treatment has been effective in controlling apple blue mold [85], citrus green mold [45], loquat anthracnose rot [88], and postharvest anthracnose pathogen of banana [77]. The findings underscore the substantial promise of *Pichia* strains as viable, environmentally sustainable alternatives to chemical fungicides for mitigating postharvest diseases in fruits and vegetables. The biological control activity of yeasts has been evaluated for the control of various plant diseases and mold growth in agricultural products. For example, Campanella and Miceli [89] studied the efficacy of yeasts in controlling *Fusarium wilt* of lentil, while Druvefors et al. [33] investigated their potential in suppressing mold growth in wheat. Yeasts have also been explored as a biocontrol agent against *Fusarium fujikuroi* in rice [90]. These findings highlight the potential of yeasts as a natural and sustainable alternative to chemical pesticides for plant disease management.

2.1.3. *Metschnikowia spp.*

The genus *Metschnikowia* includes globally distributed phylloyeasts and nectar yeasts, which have great potential as natural and successful biological control tools. *Metschnikowia* sp. can produce an antibacterial pigment called pulcherrimin and has been studied extensively for its use in biological control [50,73]. Among these, *Metschnikowia fructicola* and *Metschnikowia pulcherrima* have been subject to the most comprehensive investigations regarding biological control, exhibiting the capacity to impede a diverse array of postharvest and plant rot diseases [50,91]. Some strains from *Metschnikowia* spp. have been proved available against *P. digitatum* [48], gray spot rot *(Pestalotiopsis vismiae)* [92], *P. italicum,* and *Geotrichum citri-aurantii* [14], brown rot of peaches [93]. The use of *Metschnikowia* as a biocontrol agent has several advantages, including its non-toxicity to humans and the environment, its low cost, and its ability to colonize plant surfaces, leading to long-lasting protection against plant pathogens. Some species of *Metschnikowia* have been studied for their potential use in food and beverage production [94]. For instance, *M. pulcherrima* is recognized for its proficiency in generating diverse flavor and aroma compounds, rendering it a favored yeast strain within the non-*Saccharomyces* species, particularly in the context of winemaking applications [95].

2.1.4. *Debaryomyces spp.*

"Killer strains" are specific yeast variants adept at producing a proteinaceous killer toxin, lethal to susceptible strains lacking immunity. This phenomenon, termed the killer phenomenon, spans yeast genera: *Debaryomyces*, *Hanseniaspora*, *Kluyveromyces*, *Pichia*, *Saccharomyces* and *Candida* [96]. Within these, certain strains are identified as "killer strains" due to their toxin-producing capacity. *Debaryomyces* has exhibited efficacy in mitigating postharvest diseases in horticultural crops, such as apple and pear [54,97], muskmelon [98], jujube [99], persian lime [52], kiwifruit [100], mango [53], etc. Among antagonistic yeasts, *D. hansenii* exhibits remarkable resilience in withstanding severe environmental stressors, encompassing low pH levels, suboptimal temperatures, and heightened osmotic pressures [101]. The potential inhibitory effect of *D. hansenii* as an effective biocontrol agent against some post-harvest plant pathogens such as *B. cinerea* [102], *P. digitatum* on Tarocco orange fruits [103], blue mold caused by *P. italicum* on lime [104], *Colletotrichum gloeosporioides*, causing anthracnose on papaya fruits [12] has been demonstrated in several studies.

2.1.5. *Hanseniaspora spp.*

Hanseniaspora genus was formerly known as *Kloeckera* but was renamed to *Hanseniaspora* in 2003. *Hanseniaspora* species are found in a variety of habitats, including soil, fruit, flowers, and wine. They are known for their ability to produce fruity and floral aromas and flavors in fermented beverages, such as wine, beer, and cider [105]. Glucose and other sugars can be fermented by some *Hanseniaspora* species, and ethanol and other volatile compounds are produced during the fermentation process. *Hanseniaspora* species have been found to play a role in spontaneous wine fermentations, where they may be present in the early stages of fermentation before being outcompeted by other yeast species [106]. One significant advantage of using *Hanseniaspora* as a biocontrol agent is their natural presence on fruits and in the environment, as well as their generally recognized as safe (GRAS) status. Some species of *Hanseniaspora* have been investigated their potential as biocontrol agents against fungal pathogens that can infect crops. For example, Delgado et al. [16] noticed that the yeast strain *Hanseniaspora osmophila* (strain 337) was tested *in vitro* as a good biocontrol agent against *Botrytis* bunch rot and summer bunch rot in table grapes. *H. osmophila* (strain 337) demonstrated a mycelial inhibition effect of *B. cinerea*, *Aspergillus* spp., *P. expansum*, and *R. stolonifera* by their volatile organic compounds (VOCs) [16]. Similarly, *Hanseniaspora opuntiae*

(CCMA 0760) showed an antagonistic effect against gray mold in grapes caused by *B. cinerea* [59]. The mechanisms by which *Hanseniaspora* species exert their biocontrol activity are not yet fully understood, but they may involve the production of antimicrobial compounds, competition for nutrients and space with the pathogen, and as previously mentioned the production of VOCs. Tejero et al. [107] showed that two antagonistic strains of *Hanseniaspora*, *H. opuntiae* L479 and *Hanseniaspora uvarum* L793, produced VOCs that inhibited the growth and mycotoxin production of *Aspergillus flavus*, a fungal pathogen that produces carcinogenic aflatoxins. These authors also observed that the *Hanseniaspora* strains influenced the expression of the regulatory gene of the aflatoxin pathway (*aflR*), which is essential for the production of aflatoxins by *A. flavus* [107]. This suggests that *Hanseniaspora* species may interfere with the regulation of toxin biosynthesis in the fungal pathogen. In another study, Cordero-Bueso et al. [58] substantiated that *H. uvarum* and *Hanseniaspora clermontiae* exhibited inhibitory effects on the proliferation of *B. cinerea*, a fungal pathogen known to induce gray mold disease in a diverse array of crops. The authors ascribed the biocontrol efficacy of these yeasts to their capacity for synthesizing cell wall-degrading enzymes and emitting VOCs that hindered the growth.

2.1.6. Cryptococcus spp.

Cryptococcus species have garnered attention for their potential use as biological control agents against postharvest diseases in peach, pear, apple [61]. These species include *Cryptococcus laurentii*, *Cryptococcus flavescens*, and *Cryptococcus albidus* strains [63,108,109]. Among them, *C. albidus* strain achieved registration as a biological control agent in 1997 [110] and has been demonstrated as an efficacious antagonistic yeast capable of notably eliciting resistance in a diverse array of fruits [109]. A large number of studies have reported the antagonistic effect of *C. albidus* on pathogenic fungi, such as gray mold and blue mold on apple, *Botrytis* of strawberries, and postharvest pears disease [86,111]. Research has centered on mechanisms contributing to enhanced disease resistance in antagonistic *C. albidus* yeast, encompassing assessments of enzyme activity, gene expression, secondary metabolites, and plant hormones. Tang et al. [62] elucidated the correlation between ethylene and the resistance elicited by the biocontrol yeast *C. laurentii* against gray mold of *B. cinerea* infection in cherry tomato. Transcriptome sequencing of cherry tomato fruits pre-induced with *C. laurentii* revealed a significant up-regulation in the expression of several key genes involved in ethylene signal transduction pathways, including *SlCHI9*, *SlGlub*, *SlPAL3*, *SlPR1*, and *SlPR5*. In addition, the mechanism by which *C. laurentii* antagonist yeasts to enhance host fruit disease resistance also includes key enzyme activities and accumulation of antimicrobial secondary metabolites. The combined application of *C. laurentii* FRUC DJ1 and carboxymethylcellulose elicited the activities of defense enzymes, including chitinase, β-1,3-glucanase, peroxidase, polyphenol oxidase, and phenylalanine ammonialyase [109]. This response served to fortify the fruits' resistance against the green mold of postharvest grapefruit by the germination of *P. digitatum* conidia.

2.1.7. Other antagonistic yeasts

Aureobasidium is a genus of fungi that has been studied for its potential as a biocontrol agent for pre- and postharvest disease management. The most commonly studied species in this genus as biocontrol agents are *Aureobasidium pullulans* [41,112]. Research has shown that *A. pullulans* can be effective in controlling various post-harvest diseases, including gray mold, blue mold, and green mold on fruits and vegetables. The mechanism of action is thought to be through the production of antibiotics and competition with fungi for nutrients and space. Aureobasidin A is a natural product produced by *A. pullulans* that has been shown to have antifungal activity against a variety of plant pathogenic fungi [113]. In addition to this, *A. pullulans* also produces a range of enzymes that can help to break down plant cell walls and make nutrients more accessible. This can be particularly useful in the context of postharvest fruits and vegetables, where the presence of these enzymes can help to prevent spoilage and extend shelf life [42]. Overall, the use of *A. pullulans* as a biocontrol agent is a promising approach for reducing the use of synthetic fungicides and improving the quality of produce.

Kluyveromyces yeasts are used in the production of fermented foods and beverages, such as bread, beer, and wine. Some species of *Kluyveromyces* have also been studied for their potential as probiotics and for their antimicrobial properties. Alasmar et al. [114] evaluated the *in vivo* application of *Kluyveromyces marxianus* QKM-4 strain in tomato and grape. VOCs produced by QKM-4 strain were able to significantly limit the fungal growth of 17 fungal species belonging to *Aspergillus, Penicillium, and Fusarium genera.* It was also observed that the QKM-4 strain had the ability to remove two mycotoxins, ochratoxin A (OTA) and deoxynivalenol (DON), which are produced by some of the key toxigenic fungi [114]. This was demonstrated through *in vitro* testing, which showed that the strain was able to significantly reduce the levels of these mycotoxins. In addition, *Kluyveromyces lactis* is a well-known producer of killer toxins, which have been shown to be effective against a wide range of fungal species, including those that are responsible for food spoilage and plant diseases. Killer yeasts are of interest to researchers and industry because they have potential applications in controlling spoilage and pathogenic yeasts in food and beverage production. By using killer yeasts, it may be possible to control the growth of undesired yeast strains and improve the quality and safety of fermented foods and beverages. Some strains of *Saccharomyces* strains are killer strains. *Saccharomyces* is a genus of yeasts that includes many species commonly used in the production of bread, beer, wine, and other fermented foods. One of the most well-known species is *Saccharomyces cerevisiae*, which have been proved to be effective in controlling apple blue mold disease and grape gray mold [115,116]. Certain species of *Rhodotorula* species, including *Rhodotorula glutinis* and *Rhodotorula mucilaginosa*, have been shown to be effective for the biocontrol of post-harvest pathogens such as *B. cinerea* and *P. digitatum* [117,118]. In addition, certain species from *Sporidiobolus* and *Wickerhamomyces* have been investigated for its potential use in post-harvest disease management. Several studies have shown promising results regarding the efficacy of *Sporidiobolus* in controlling post-harvest diseases in various crops such as strawberries, grapes, and tomatoes [66,119,120]. *Sporidiobolus* is generally considered safe for human consumption, and there are no reported cases of adverse effects associated with its use in post-harvest disease management. *Wickerhamomyces anomalus* WRL-076 is a yeast strain that has been studied for its biocontrol properties against *A. flavus*, a fungus known to produce the carcinogenic toxin aflatoxin [121]. The biocontrol efficacy of *W. anomalus* WRL-076 against *A. flavus* and its ability to decrease the expression of genes involved in aflatoxin biosynthesis make it a promising candidate for further research and potential use in agricultural applications to reduce the risk of aflatoxin contamination in crops.

Identification of organisms at the species level is a critical aspect of categorization, and molecular techniques are important for achieving this goal. In a recent study, the effective yeast isolate *H. guilliermondii* YBB3 was identified as *H. guilliermondii* using 26S rDNA sequencing [57]. This methodology has also been used in previous studies, such as Cordero-Bueso et al. [58], to identify yeast species. Molecular analysis using 16S RNA also adapted to examine the biocontrol efficacy of some yeast isolates [122]. Ongoing investigations are presently delving into the prospective utilities of antagonistic yeasts across diverse domains. These pursuits are closely linked with concurrent inquiries scrutinizing the modalities by which they impede the proliferation of other microorganisms.

2.2. Mechanisms of control of unwanted microorganisms by yeasts

The use of antagonistic yeasts as biological control agents in crop protection, particularly in fruit and vegetable products, is considered a promising alternative to chemical fungicides, as they are effective in controlling pre- and post-harvest fungal diseases with less environmental impact. Modulation of interactions of antagonistic yeasts with the environment and host through, for example, spatial and nutrient distribution, synthesis and secretion of antifungal substances (VOCS, toxins, enzymes, antibiotics, etc.), mycoparasitism, induction of plant immune responses to pathogens, are among the mechanisms of action of antagonistic yeasts which will be described briefly below. The reactive oxygen species (ROS) production, biofilm formation and quorum sensing are also responsible for their antagonistic activity suppressing postharvest fungal pathogens on fruits.

2.2.1. Competition for nutrients and space

The most prevalent and crucial mode of action involves competing for nutrients, space, and oxygen. Postharvest fruits are vulnerable to physical damage that can provide entry points for putrefactive pathogens. During the first 24 h of postharvest storage, yeast antagonists can exert their most critical modes of action in limiting the growth and spread of postharvest fungal diseases [82]. Living plants secrete organic acids, vitamins, minerals, and other easily utilized compounds, which serve as their primary nutrient source. Further, yeasts can use most of the carbohydrate and nitrogen sources for cell growth. By competing for nutrients and niche exclusion, yeast antagonists can outcompete pathogenic fungi for available resources, physically occupy wound spaces, and reduce nutrient availability at the wound site, thus limiting fungal spore germination, growth, and infection [82]. The attachment of antagonistic yeast to pathogenic mycelia also increases nutrient competition opportunities and impedes the pathogen infection process. Therefore, utilizing yeast antagonists as biocontrol agents during postharvest storage can be highly effective in preserving the quality and safety of harvested fruits and vegetables.

The colonization of fruit wounds by antagonists and effective competition with pathogenic fungi and bacteria are also influenced by other factors, including natural non-pathogenic microorganisms at the wound, antagonist concentration, the amount of available nutrients, temperature and humidity [123–125]. Bencheqroun et al. [126] observed that antagonist (*A. pullulans* strain Ach1-1) could reduce germination percentages of *P. expansum* conidia at lower apple juice concentration (0–5%). But the addition of juice to a final concentration of 5 % resulted in a decrease in the inhibitory potency of strain Ach1-1. Ach1-1 was effective in protecting postharvest wounded apples against *P. expansum*. However, the protective effect was significantly reduced when high concentrations of exogenous sugars, vitamins, and amino acids were applied, particularly when apple amino acids were applied at the wound site [126]. The requirement for physical contact between pathogen and antagonist is a key determinant of effective antagonist-mediated control. The germination of *Penicillium digitatum* and *Penicillium italicum* is clearly decreased without competition for space, however, when *P. agglomerans* (antagonistic bacteria) is in close contact with pathogen, germination of *Penicillium* conidia is almost completely inhibited [127]. These findings underscore the importance of direct pathogen-antagonist interaction for effective biocontrol.

2.2.2. Secretion and synthesis of antibacterial compounds

A number of antifungal VOCs produced by biocontrol yeasts have been associated with fungal inhibition, i.e., several alcohols and esters (ethyl acetate, isoamyl acetate, phenylethyl acetate, isobutyl acetate and ethyl propionate) [128]. Some VOCs have been shown to be very effective in inhibiting the growth of postharvest fungi *in vivo*. VOCs, produced by *Sporidiobolus pararoseus*, *C. sake*, *Hanseniaspora*, *W. anomalus*, *M. pulcherrima*, *A. pullulans* and *S. cerevisiae* have been proven to significantly inhibit the growth of such pathogens as *B. cinerea*, *C. acutatum*, *P. expansum*, *P. digitatum* and *P. italicum* [129]. It has also been found that some killer toxins secreted by yeasts are active not only against sensitive yeasts but also against molds [130]. In addition, some antagonistic yeasts like *Pichia membranaefaciens* and *Kloeckera apiculata* have an ability to secrete hydrolytic enzymes, such as chitinase and β-1, 3-glucanase, which can damage the fungal cell wall after induction [131].

Some antagonistic yeasts produce natural antibiotics that can be used as an alternative to synthetic antibiotics. *M. pulcherrima,* exhibiting strong antagonistic activity against *B. cinerea* growth, synthesizes 35 metabolites such as piperideine and protoemetine (alkaloids), *p*-coumaroyl quinic acid (phenylpropanoid), β-rhodomycin (antibiotic), hexadecanedioic acid (long chain fatty acid) or taurocholic acid (bile acid) [91]. *Aureobasidium* strains with the ability to produce non-volatile metabolites such as polysaccharides, lytic enzymes, siderophores and antibiotics, are used as antagonistic agent against gray mold of tomato [132]. Another way in which *Aureobasidium* strains can suppress gray mold is by inhibiting the activity of xylanase, an enzyme produced by *B. cinerea* that is involved in the degradation of plant cell walls and contributes to the virulence of the pathogen. By producing compounds that inhibit xylanase activity, *Aureobasidium* strains can reduce the ability of *B. cinerea* to cause disease.

Antagonistic yeasts are also capable of producing substances with antimicrobial properties including organic acids [133], hydrogen peroxide [134], and extracellular proteases [135]. These compounds can effectively restrict the growth of harmful microorganisms and thereby prevent infections.

2.2.3. Mycoparasitism and the secretion of lytic enzymes

Mycoparasitism is considered a major contributor to fungus-fungus antagonism. Mycoparasitism is a type of antagonistic interaction between two fungi where one fungus, called the mycoparasite, feeds on another fungus, called the host or prey, through direct attachment and secretion of lytic enzymes. The mycoparasite can derive nutrition from the host, which can lead to the death of the host.

Mycoparasites can be a potential tool for biocontrol of fungal diseases in crops and can also play a role in the natural regulation of fungal populations in the environment. Some examples of mycoparasites include *Trichoderma* species, which are commonly used as biocontrol agents against various plant pathogens, and *S. cerevisiae*, which has been shown to parasitize on filamentous fungi in certain conditions [136,137]. During mycoparasitism, the yeasts secrete a variety of enzymes to degrade the fungal pathogen cell wall, and these enzymes play a crucial role in biocontrol. β-1,3-glucanase (GLU) breaks down the β-1,3-glucan component of the fungal cell wall, which is an important structural component that provides rigidity to the cell wall. Chitinases hydrolyze chitin, another important component of the fungal cell wall. Proteases also play an important role in breaking down proteins [138]. For example, the MfChi chitinase of *Metschnikowia fructicola* AP47 has been reported to play a primary role in its antagonistic activity against *Monilinia fructicola* and *Monilinia laxa in vitro* and on peaches [93].

Overall, mycoparasites and their enzymatic activities hold promise for the control of fungal pathogens in agriculture and other settings. However, mycoparasitism in yeasts has been poorly studied. Further research is needed to fully understand the mechanisms of mycoparasitism.

2.2.4. The role of biofilm formation and quorum sensing

The ability of antagonistic yeasts to effectively adhere, colonize, and multiply on both intact and injured fruit surfaces has been attributed to their capacity for biofilm formation, which involves the creation of microcolonies embedded in a matrix of hydrated proteins, nucleic acids, and polysaccharides. Quorum sensing (QS) is a mechanism by which bacteria, fungi, and other microorganisms can communicate and coordinate their activities to achieve certain goals such as the colonization of a host, sporulation, the formation of biofilms, or the expression of virulence factors. QS is frequently noted in yeasts' biofilm formation. It constitutes an intricate intercellular signaling system facilitated by small diffusible molecules. These molecules, known as quorum sensing molecules (QSMs), accumulate in the environment as microbial populations grow, triggering specific gene expression upon reaching a threshold concentration [139]. QS has demonstrated effective control of postharvest pathogens in biocontrol systems by facilitating cell-to-cell communication, enabling individual cells to regulate their phenotype in response to the concentration of extracellular quorum-sensing molecules [140]. For example, phenylethanol, which acts as a QS molecule, induces the adherence and biofilm formation of *K. apiculata* on citrus fruit, leading to the development of an extracellular matrix that creates a mechanical barrier between the pathogen and the wound surface [141]. Some antagonistic yeasts used for biocontrol against fruit diseases were suggested to utilize biofilm formation as an important mode of action [142]. The biocontrol efficacy of a biofilm-forming *Pichia kudriavzevii* strain is tightly correlated with the morphological change of yeast cells. *P. kudriavzevii* in the biofilm form exhibits significantly increased tolerance to heat and oxidative stresses, as well as improved biocontrol efficacy against postharvest diseases on pear fruit compared to the yeast-like form [143]. Cordero-Bueso et al. [58] isolated 26 yeast species from grape, 20 of which were found to have antagonistic action against all molds through several mechanisms of action, including nutrient and space competition, cell wall degrading enzymes, and biofilm formation. However, in some instances, the formation of biofilm can result in an unforeseen pathogenic response. Although biofilm-forming strain of *Pichia fermentans* effectively controls brown rot when inoculated into apple surfaces and within apple wounds, its colonization of peach fruit tissue results in rapid decay of the fruit tissues through a transition from budding growth to pseudohyphal growth, even in the absence of a phytopathogenic strain of *M. fructicola* [144]. The association of unexpected pathogenic behaviors with unique biofilm structures that promote virulence factor production remains unclear. However, these findings emphasize the significance of studying biofilms to better comprehend their role in infection.

2.2.5. Induced systemic resistance of fruit host

The existence of adaptive defense mechanisms in plants allows pathogens that manage to break through the physical barriers of plant tissue, such as wax, cuticle, and thick cell walls, to be recognized by the plant host and thus trigger and activate innate plant immunity [145]. This latent defense mechanism, known as induced systemic resistance (ISR), is affected by biological or abiotic agents, such as microorganisms and chemicals [146]. A variety of biochemical defense responses are induced by antagonistic yeasts on fruit and vegetable wound surfaces, in addition to nutritional and spatial competition. In several studies, it was proven that antagonistic yeasts, such as *C. oleophila*, *P. membranefaciens*, *Rhodosporidium paludigenum,* and *M. fructicola* may induce systemic resistance in plants [81]. For instance, *P. guilliermondii*-treated peach fruit gained improved disease resistance against *R. stolonifer* and *P. expansum* infection by increasing the activities of defense-related enzymes and the content of salicylic acid [147]. *C. oleophila* application to surface wounds or to intact 'Marsh Seedless' grapefruit elicited systemic resistance against *P. digitatum*, the main postharvest pathogen of citrus fruit [81]. Despite these findings, the capacity of different yeasts to induce ISR in plants has not been systematically investigated, and the underlying mechanisms are not well understood.

2.2.6. Other mechanisms

Yeasts can also enhance the production of ROS as a means of inhibiting the growth of postharvest pathogens [91]. By withstanding oxidative stress, antagonistic yeasts can maintain their viability and continue to exert their inhibitory effects on postharvest pathogens

[148]. Yeasts also gained importance in prevention and decontamination of mycotoxin [149]. Yeasts possess immense potential as biocontrol agents in postharvest systems due to their ability to offer multiple modes of action and their reputation for being safe and eco-friendly. Table 2 presents the actions carried out within a tritrophic interaction system involving an antagonistic microbe, a fungal pathogen, and a host fruit, which are aimed at controlling postharvest diseases.

2.3. *Enhancing biocontrol efficacy and viability*

Biocontrol yeasts used to control postharvest diseases encounter a variety of environmental conditions that affect their ability to survive and thus their efficacy. In some cases, biocontrol agents are applied in the field before harvest, which exposes them to a wide range of environmental stresses, such as extreme temperature, oxidative stress, freeze/spray drying for their preparation, solute stress, and extreme pH in biological control systems. Survival and proliferation in injured tissue contribute to postharvest biological control effectiveness [157]. Nonetheless, the surplus of ROS in fruit tissues during the injury process could impact the efficacy of yeast [158]. The pH value of medium and fruit tissue can also affect the growth and the vitality of biocontrol yeasts. Therefore, enhancing the tolerance to unfriendly environment is a strategy to improve the survival ability and biological antagonism of yeasts. A diagram of promising strategies to improve the efficacy of antagonistic yeasts is shown in Fig. 2.

Previous studies have shown that cold adaptation regulates yeast membrane fluidity in response to dry environments, while mild heat shock enhances tolerance to subsequent lethal heat stimulation and oxidative stress, suggesting that mild stress enhances the tolerance of biocontrol agents to subsequent lethal stress [159]. Sublethal oxidative stress has also been reported to enhance the ability of yeast to tolerate subsequent adverse environmental conditions [160]. In addition, the salt adapted *R. paludigenum* showed better viability than the un-adapted cells in low water activity medium and in frozen environment. Wang et al. [161] have conducted research to enhance the acid tolerance of *R. paludigenum*, by modifying it with malic and lactic acid. Therefore, yeast preadaptation to abiotic stress may have positive implications for improving the effectiveness of antagonistic yeasts, which will be more effective in controlling postharvest spoilage in fruits and vegetables under a wider range of environmental conditions, thereby reducing economic losses.

The combination with other antimicrobial compounds is also one of the effective ways to improve the performance of biological control. The synergistic effects of methyl jasmonate and salicylic acid, the plant growth regulator and defense activator respectively, which have been observed to produce a synergistic effect with antagonistic yeasts for safeguarding various fruits such as apple, pear, peach, and loquat [162]. The combined application with biomacromolecules with good compatibility, such as, chitosan, alginate, gum, starch, or cellulose is also a good choice to improve the biological control ability of yeasts [163]. There are also studies about the function of metal ions (magnesium, ferrous, and zinc), from which addition enhanced the antagonistic activity and biomass production ability of yeast [164]. Glucose is also widely used as a protectant for biological control agents to withstand various stresses [165].

Table 2

Representative modes of action by antagonistic yeasts in postharvest biocontrol systems involving pathogen-fruit host-yeast interactions.

Modes of action	Antagonistic yeasts	Target pathogens	Host fruits	References
Competition for nutrients and space	*P. anomala, D. hansenii, H. guilliermondii*	*P. Digitatum*	Citrus	[150]
	A. pullulans GE17, *Meyerozyma guilliermondii* KL3	*P. expansum* DSM62841, *P. digitatum* DSM2750	Apple, lemon	[151]
	W. anomalus	*P. expansum*	Apple	[152]
Synthesis of antifungal compounds	*M. pulcherrima*	*B. cinerea*	Tomato, grape, apple	[91]
	A. pullulans, A. subglaciale, A. melanogenum	*B.cinerea*	Tomato	[132]
	P. membranaefaciens, Kloeckera apiculate	*M. fructicola*	Plum	[131]
	P. kudriavzevii L18	*P. glabrum*	Grape	[42]
Mycoparasitism	*W. anomalus, M. guilliermondii*	*C. gloeosporioides*	Papaya	[130]
	D. hansenii	*Fusarium proliferatum*	Muskmelon	[98]
The secretion of lytic enzymes	*A. pullulans* PL5	*M. laxa, B. cinerea, P. expansum*	N/A	[135]
	P. membranaefaciens, K. apiculate	*M. fructicola*	Plum	[131]
Biofilm formation and quorum sensing	*Zygoascus meyerae* L29	*P. glabrum*	Grape	[42]
	K. apiculata 34-9 strain	*P. italicum*	Citrus	[141]
	Torulaspora indica DMKU-RP31, *T. indica* DMKU-RP35, *Pseudozyma hubeiensis* YE-21	*L. theobromae, C. gloeosporioides*	Mango	[153]
	D. nepalensis	*A. alternate*	Jujube	[99]
Induced systemic resistance of host	*K. apiculate*	*P. Expansum*	Apple	[22]
	P. membranefaciens	*R. stolonifera*	Peach	[154]
	D. hansenii	*R. Stolonifera*	Strawberry	[155]
	P. membranefaciens	*P. italicum, P. digitatum*	Citrus	[156]
Enhanced production of ROS	*M. fructicola, C. oleophila*	N/A	Citrus, apple	[134]
	M. pulcherrima	*B. cinerea*	Tomato, grape, apple	[91]

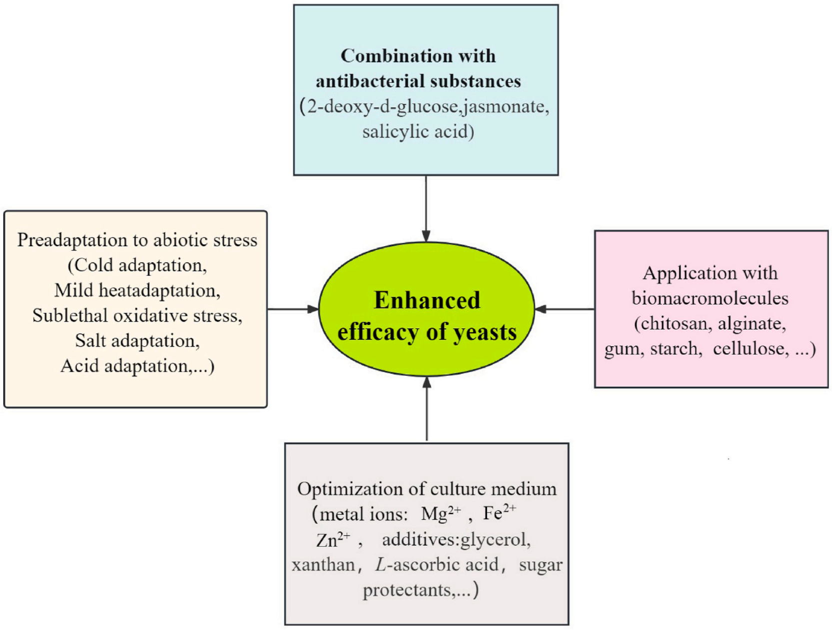

Fig. 2. Diagram of promising strategies to improve the efficacy of antagonistic yeasts.

Table 3
Examples of biopreservation of processed food by antagonist yeasts.

Food types	Antagonistic yeasts	Mode of action	Targeted pathogens	References
Wine	*M. pulcherrima*	Secretion of lytic enzymes, VOCs	*Mucor, Botrytis, Aspergillu, Penicillium*	[166]
Cheese	*D. hansenii* B9010	Secretion of mycin, competition for nutrients and space, Production of aromatic compounds with antifungal activity	*Aspergillus* sp., *B. fulva, B. nivea, Cladosporium* sp., *Eurotium chevalieri, Penicillium candidum, Penicillium roqueforti*	[167]
Red grape juice	*C. pyralidae*	The killer toxins CpKT1 and CpKT2 killer toxins	*Brettanomyces bruxellensis*	[168]
Apple juice	*R. mucilaginosa*	Degradation of the mycotoxin patulin, competition for nutrients	*Penicillium*	[20]
Coffee	*S. cerevisiae* UFLA YCN727, *S. cerevisiae* UFLA YCN724, *Candida parapsilosis* UFLA YCN448, *P. guilliermondii* UFLA YCN731	Production of organic acids, volatile compounds, Secretion of hydrolytic enzymes	Spoilage bacteria and fungi	[169]
Coffee	*S.cerevisiae* CCMA 1302	Volatile organic compounds production, biofilm formation	*Aspergillus carbonarius*	[170]
Dry-fermented Sausages	*D. hansenii* 280	Competition for nutrients and space, production of soluble or volatile compounds	*Penicillium verrucosum*	[171]
Dry-cured ham	*D. hansenii*	Competition for nutrients and space, compounds with antimycotic activity are produced, degrading mycotoxins to the less toxic compounds	*P. nordicum*	[172]
Cheese	*D. Hansenii*	production of volatile compounds	*Cladosporium inversicolor, Cladosporium sinuosum, Fusarium avenaceum, Mucor racemosus, P. roqueforti*	[133]
Smear Soft Cheese	*D. hansenii* (GMPA, 304)	Synthesis of proteolytic enzymes	N/A	[173]
Fermented milks	*S. cerevisiae,* *K. marxianus*	Competition for nutrients and space, Production of mycocin	*Escherichia coli*	[174]

3. Biopreservation of yeasts in processed foods

Yeasts occur in all environments and have been described as potent antagonists of various plant pathogens. Although there is a great deal of research on the use of yeasts as biocontrol agents to protect agricultural products, some research has also contributed to the use of yeasts to inhibit foodborne bacteria and fungi. The application of yeast in processed foods was first reflected in the control and participation in the fermentation process, such as wine, beer, bread, or cheese. As shown in Table 3, some antagonists used for postharvest control of fruits and vegetables also have great antimicrobial potential in food processing, which indicates that the good characteristics of biocontrol yeasts can be used as a favorable reference for the use of yeast to control food quality in the future. In this section, current uses of yeasts in processed foods such as juices, wine, coffee, dry-cured meat products, dairy products will be introduced.

3.1. Plant-based foods

3.1.1. Wine

Unregulated proliferation of microorganisms prior to, during, or following wine fermentation has the potential to modify the chemical makeup of the final product, thereby diminishing its sensory characteristics such as its appearance, aroma, and flavor. Sulfur dioxide (SO_2) is considered an essential tool for winemakers and the commonly used chemical additive in the wine industry due to its low cost, antioxidant and anti-microbial properties [175]. However, excessive use of chemical preservatives degrades the quality of wines and faces increasing consumer resistance. The World Health Organization (WHO) promotes alternative methods to diminish or eliminate the use of SO_2 in wine production. Therefore, biological preservation using yeast and its derived metabolites is currently being considered as an alternative to chemical preservation.

S. cerevisiae is the primary yeast responsible for conducting alcoholic fermentation during the brewing process. The ability of *S. cerevisiae* to tolerate higher concentrations of ethanol compared to other microorganisms is a major factor that contributes to its dominance during alcoholic fermentation. Most studies have validated the use of *S. cerevisiae* as starter cultures to prevent the growth of spoilage yeast and bacteria in wine fermentations [176]. Additionally, *S. cerevisiae* has also been proposed as an alternative strategy to control mycotoxins. *S. cerevisiae* DISAABA1182 was identified with an ability to inhibit the growth of *A. carbonarius* and *Aspergillus ochraceusboth in vivo* and *in vitro* [177]. Its capability to suppress OTA production was investigated through the transcriptional regulation of OTA biosynthetic genes *pks* (polyketide synthase). The effect of *Saccharomyces cerevisiae* strains to produce OTA, DON and zearalenone (ZEA) is affected by different interacting environmental conditions, e.g., temperature, moisture activity, pH values [178].The *Saccharomyces eubayanus* killer toxin isolated in a wine-like medium can break down the cell walls of *Brettanomyces bruxellensis*, *P. membranifaciens*, *M. guilliermondii*, and *Pichia manshurica*, leading to necrotic and apoptotic death in a dose-dependent manner [179]. Furthermore, *S. cerevisiae* produces peptides derived from glyceraldehyde-3-phosphate dehydrogenase (GAPDH) that have antimicrobial activity against a variety of microorganisms, including bacteria and fungi. These peptides are thought to play a role in the yeast's defense system, protecting it from potential pathogens that could compete for resources during fermentation [180].

Non-*Saccharomyces* yeasts are naturally present in grapes and vineyards and typically dominate the early stages of spontaneous fermentation before *S. cerevisiae* takes over and completes the fermentation process. Non-*Saccharomyces* yeasts are now recognized for their various contributions to wine production, including increasing the complexity of wine aroma, reducing the ethanol content of wine, and aiding in the prevention of wine spoilage [181]. Research has investigated the potential of non-*Saccharomyces* yeasts as bioprotective agents in wine, such as *Torulaspora delbrueckii* [182], *M. pulcherrima* [183], *W. anomalus* [181]. The introduction of non-*Saccharomyces* yeast species such as *T. delbrueckii* and *Lachancea thermotolerans* during the early stages of vinification had a comparable impact to the use of SO_2, in terms of restraining the growth of harmful microorganisms [184]. CpKT1 and CpKT2 are killer toxins that have been isolated from the wine yeast *C. pyralidae* [167]. These toxins can inhibit the growth of various yeast species, including *B. bruxellensis*, which is a common wine spoilage yeast.

3.1.2. Juices

While there has been extensive research on the biological control of postharvest fruits and vegetables using antagonistic yeasts, the focus of research on the biological protection of fruit juice has mainly been on grape juice [185]. However, there has been some recent research on the use of antagonistic yeasts for the biological protection of other types of fruit juice. Additionally, some research has focused on the use of yeast-based biocontrol agents to improve the shelf life and quality of fruit juices during storage. A survey carried out by Richards et al. [186] has demonstrated the potential use of *D. hansenii*, *P. guilliermondii*, and *Pseudozyma* spp. as natural preservatives to inhibit the growth of *Salmonella* in cantaloupe juice and wounds. In the study conducted by Chan and Tian [187], interactions between the antagonistic yeasts *P. membranefaciens* and *C. albidus*, along with three fungal pathogens—*M. fructicola*, *P. expansum*, and *R. stolonifer*—were explored on both apple juice agar plates and in apple wounds. *P. membranefaciens* demonstrated superior attachment to fungal hyphae, a process effectively inhibited by sodium dodecyl sulfate (SDS) and β-mercaptoethanol. Moreover, culture extracts from *P. membranefaciens* exhibited elevated levels of β-1,3-glucanase and exo-chitinase activities but lower endo-chitinase activity compared to *C. albidus*. The findings revealed that the yeasts were able to successfully impede the growth of the fungal pathogens by utilizing a combination of tenacious attachment and the secretion of extracellular lytic enzymes.

Many yeasts can degrade mycotoxins, including patulin, which frequently contaminates fruits and fruit-derived products. *R. mucilaginosa* and its orotate phosphoribosyltransferase enzyme have potential to reduce patulin in apple juice [20]. A strain of *Rhodosporidium kratochvilovae*, LS11 strain, also exhibits a detoxification effect on patulin, suggesting a novel biodegradation pathway [188]. Yue et al. [189] suggested that inactivated yeast strains can effectively reduce the amount of patulin in apple juice by more than

50 % within 24 h of treatment. This indicates that inactivated yeast strains have the potential to be used as a method for patulin reduction in apple juice processing. However, it is important to note that the efficacy of patulin reduction may depend on various factors, such as the initial concentration of patulin in the juice, the specific yeast strains used, and the treatment conditions. Additionally, the impact of inactivated yeast treatment on other quality parameters of apple juice, such as flavor, aroma, and nutritional content, also needs to be evaluated to ensure that the final product meets the desired quality standards. The optimal conditions for the use of inactivated yeast strains to reduce patulin in apple juice processing need to be determined so that the resulting product maintains high quality and safety standards.

3.1.3. Coffee

The use of antagonistic yeasts in coffee processing is a promising approach to reduce the use of synthetic fungicides and improve coffee quality. In addition to wine production, *S. cerevisiae* is highly used in coffee production and in the fermentation of coffee waste grounds [190]. *S. cerevisiae* is used to ferment the coffee cherries before they are roasted in coffee production. Besides *S. cerevisiae*, some of the most identified yeast genera in coffee fermentation and processing include *Pichia*, *Candida*, *Saccharomyces*, *Rhodotorula, Hanseniaspora, Kluyveromyces* and *Torulaspora* [169,191]. In a study investigating coffee fermentation using three *S. cerevisiae* strains as starter cultures (i.e., bakery, white, and sparkling wine yeasts), a significant reduction in the production of non-desired compounds, including β-N-alkanoyl-5-hydroxytryptamides (C-5HTs), cafestol, and kahweol, was observed [192]. This highlights the potential role of yeasts in controlling the production of unwanted compounds during coffee fermentation. *H. uvarum* and *P. kudriavzevii* have been characterized as predominant strains in the yeast community during the wet fermentation of coffee beans [193], and the potential antagonism of *P. kudriavzevii* with *Bacillus cereus* have also been recorded [194].

Filamentous fungi, including *Aspergillus*, *Penicillium*, *Cladosporium*, and *Fusarium*, are commonly found in coffee beans and are known to produce mycotoxins. These toxic secondary metabolites can negatively impact the quality and safety of coffee, posing potential health risks to consumers. In this regard, selecting the appropriate starter for fermentation is crucial in preventing the growth of filamentous fungi, particularly those that produce OTA. *P. anomala* and *Pichia kluyveri* are both potential candidates for this purpose [195]. *In vitro* and *in vivo* assays demonstrated the effectiveness of *S. cerevisiae* CCMA strains in inhibiting ochratoxigenic fungi, with biofilm formation identified as a key mode of action [170]. Despite these findings, the role of yeasts in interactions with other microorganisms present in the fermentation process are still not well understood.

3.2. Animal origin foods

3.2.1. Dry-cured meat products

In addition to serving as a flavoring agent, yeasts possess the unique ability to proliferate to substantial populations on the surface of dry-cured meats [196]. This attribute renders them suitable candidates for acting as antagonists to combat undesirable fungi.

3.2.1.1. Dry-cured ham. Dry-cured ham is a traditional meat product that is produced by a process of salt-curing and air-drying. During the ripening period, which can last several months, an uncontrolled microbial population grows on the surface of the ham. This microbial population plays a crucial role in the development of the unique flavor and aroma of the final product. Several types of microorganisms have been identified as dominant in different types of dry-cured ham during most of the ripening period. These include molds, yeasts, and Gram-positive and catalase-positive cocci. Molds are typically the first microorganisms to colonize the surface of the ham, and they play an important role in the initial stages of ripening. As the ripening process continues, yeasts and bacteria become more dominant, and they contribute to the development of the characteristic flavor and aroma of the ham.

Several studies revealed the contribution of yeasts to the sensory characteristics of dry-cured meat products thanks to their proteolytic and lipolytic activities and their role in volatile compounds generation [197]. During ham processing, the yeast species that are most commonly isolated belong to the genera *Debaryomyces* and *Candida*, while *Cryptococcus*, *Rhodotorula*, and *Rhodosporidium* are less frequently found [198]. *D. hansenii* is the predominant species in dry cured ham isolates during processing, but this predominance becomes more remarkable in fully matured products [199]. The prevalence of *D. hansenii* in dry-cured meat products can be attributed to its moderate halophilic properties. This characteristic enables the optimal growth of *D. hansenii* in environments with a salt concentration of 3–5% [200]. However, differences in the volatile compounds generation between *D. hansenii* biotypes usually found in dry-cured meat products have been recently reported in a meat model system [201]. Several studies have reported the potential of selected antagonist yeasts to prevent the growth of unwanted molds and the accumulation of mycotoxins [201–203]. Furthermore, *D. hansenii* has been traditionally included in the European Union list of biological agents recommended for Qualified Presumption of Safety [19]. Studies have shown that *D. hansenii* has antimicrobial properties that can inhibit the growth of certain bacteria, including *Listeria monocytogenes* [204] and certain molds including *Penicillium* spp [205,206]. and ochratoxigenic molds [203] on dry-cured ham. Improper processing procedures can increase the development of mold, which can lead to negative effects such as the production of OTA. OTA has been classified by the International Agency for Research on Cancer (IARC) as a “Group B″ of human carcinogenic molecules [207]. Many studies have shown that OTA contamination can be effectively reduced or inhibited by using fine strains screened from dry-cured hams as biocontrol agents [203,208,209]. This biocontrol method is considered safe, healthy, and effective. *D. hansenii* is used as an effective biocontrol agent to enhance the safety of dry-cured hams by competing for nutrients and space with OTA producers, producing antifungal compounds, and influencing secondary metabolism, or inhibiting biosynthesis of mycotoxins [210,211]. Understanding how antagonistic yeasts work is important for improving their ability to fight toxigenic fungi. New processing and storage techniques to prevent meat spoilage bacteria may also allow yeasts to control the bacteria responsible for spoilage.

However, consideration should also be given to the effect of biocontrol agents on ham quality, such as the flavor characteristics [212].

3.2.1.2. Dry-cured sausage. The dry fermented sausages are commonly perceived as safe products from a microbiological standpoint, primarily owing to a few factors. These include the lower pH levels and water activity (a_w) of the sausages, as well as the addition of various ingredients like salt, nitrites, and spices. These constituents, in principle, can help prevent the proliferation of food-borne and spoilage microorganisms [213]. However, there are still potential risks associated with raw meat, improper storage, and cross-contamination, which can lead to foodborne illness if not properly managed.

Research on the use of yeasts for biopreservation in dry-cured sausages has been ongoing in recent years, with several studies exploring the efficacy and safety of various yeast strains. One common yeast strain used for biopreservation in dry-cured sausage is *D. hansenii* [170]. This yeast is naturally present on meat and has been shown to inhibit the growth of harmful bacteria while also improving the flavor and texture of the sausage. Twenty-two isolates of *D. hansenii* were obtained from naturally fermented sausages and evaluated for their contribution to sausage aroma by measuring the production of volatile compounds [171]. The predominant volatile compounds produced by these isolates were esters, including ethyl and methyl esters, as well as sulfur compounds, alcohols, aldehydes, and ketones. An investigation carried out by García-Béjar et al. [214] centered on the examination of yeast strains isolated from fermented sausages and observed that the identified isolates can produce volatile compounds such as esters, aldehydes, and fusel alcohols, among others. Notably, the study established that these strains exhibited biocontrol properties against mycotoxin molds, including *D. hansenii*, *Kazachstania servazzii*, and *W. anomalus*. In addition to the production of volatile compounds with antibacterial activity, the modes of action involved in the potential antifungal activity by yeasts include competition for nutrients and space or killer proteins [215]. Álvarez et al. [211] have evaluated the effectiveness of the inoculation of *E. faecium* SE920*, D. hansenii* FHSCC 253H*,* and *P. chrysogenum* CECT 20922 in controlling toxigenic molds without affecting the sensory quality of dry-cured fermented sausage (salchichón)-based medium. The role of antifungal yeast in reducing mycotoxin biosynthesis at the transcriptional level has been investigated. Two strains of *D. hansenii yeast* (FHSCC 125G and FHSCC 253H), isolated from dry-cured meat product, exhibited antagonistic activity against *Aspergillus parasiticus* by inhibiting its growth. Furthermore, the study demonstrated that the relative expression levels of the genes involved in the biosynthesis of aflatoxins, *aflR* and *aflS*, are downregulated by the yeast strains, indicating their potential as biocontrol agents to reduce aflatoxin contamination in dry-cured meat products [216]. *D. hansenii FHSCC 253H* has also been found to decrease the abundance of proteins involved in OTA biosynthesis in *Penicillium nordicum*. Additionally, the combination of yeast and rosemary has been observed to affect the cell wall integrity pathway, which is linked to mycotoxin synthesis in molds [217].

3.2.2. Dairy products

3.2.2.1. Cheese. Cheese is generally considered safe due to the presence of natural microflora such as yeasts, but mold contamination is a prevalent issue that can result in reduced cheese quality and potential mycotoxin formation [218]. Mold growth can occur throughout cheese production, leading to visible and invisible defects like mold colonization and off-flavors [219]. Some of the fungi growing on cheese may also produce mycotoxins, which lead to a food safety issue. The mold genus that contaminates cheese is mainly *Penicillium*, followed by *Aspergillus*. Therefore, there is growing interest in the use of antifungal compounds and biocontrol agents to prevent mold growth during cheese ripening, storage, and distribution.

Antagonistic yeasts have been reported to be effective biocontrol agents for preventing the growth of spoilage and pathogenic bacteria in dairy systems [220,221]. One of the most commonly used yeasts for biocontrol in dairy systems is *D. hansenii*, which is able to inhibit the growth of dairy molds such as *Aspergillus* spp., *Byssochlamys fulva*, *Byssochlamys nivea*, *Cladosporium* spp., *Eurotium chevalieri*, *P. candidum*, and *P. roqueforti* [167]. The yeast is commonly associated with smear soft cheese deacidification during ripening [173]. In the case of Danish cheese brines, *D. hansenii* strains have been found to exhibit good ability to inhibit the germination and growth of contaminating molds. The antagonistic activity of *D. hansenii* has been attributed to the production of 71 volatile compounds [133]. Surface-ripened cheeses develop a biofilm on their surface, known as the cheese rind, which is composed of a diverse community of bacteria and fungi. Yeasts are the first microorganisms to colonize the cheese surface immediately after brining, initiating the surface ripening process. This microbial community contributes to the unique characteristics of different cheese varieties [222]. A survey on soft-cheese model curds indicates that *D. hansenii* exhibited a rapid colonization of the ecosystem and suppressed the growth of *Penicillium camemberti* and other fungi during a 31-day ripening period [223]. The observed dominance of *D. hansenii* may be attributed to its capacity to thrive in the cheese-making environment characterized by high salt concentrations and low pH levels. However, *D. hansenii* was more effective at inhibiting smaller concentrations of mold in dairy products than higher concentrations of mold [167]. Further, the temperature, relative humidity, and nutrient availability also influence the antifungal efficiency of *D. hansenii* [173]. The NaCl tolerance of *D. hansenii* strains isolated from Danish cheese brines at specific temperatures has been studied [224], which provides an idea for screening yeasts with relevant traits from cheese brines for use in the cheese industry. While there has been some research on the role of antagonistic yeasts in cheese biopreservation, our understanding of their mechanisms of action and their potential use in the cheese industry is still limited.

3.2.2.2. Fermented milks. The use of killer yeasts for biocontrol purposes is still an area of active research and development, and there is still much to be learnt about their effectiveness and safety in various applications. However, their potential to control unwanted yeast growth and improve the quality and safety of fermented foods and beverages is a promising area of investigation. Fermented milk is produced by the fermentation of milk by suitable microorganisms, resulting in a decrease in pH. Depending on the dominant microbiota, fermented milk can be classified into two main types: lactic fermentation, which is dominated by lactic acid bacteria, and fungal-lactic fermentation, which involves both yeasts and lactic acid bacteria. Examples of fungal-lactic fermented milk products include Kefir, Koumiss, and Viili, among others [21]. LAB are well known, while yeasts have received less research attention and fewer commercial preparations are available. Yeasts possess natural resistance to antibacterial antibiotics, which is an advantage over bacteria. In contrast, the transfer of antibiotic resistance between lactobacilli and pathogenic bacteria poses a threat.

Common yeasts associated with fermented milks include *Kluyveromyces* spp., *Saccharomyces* spp., and *Pichia* spp [21,225]. Fernández-Pacheco et al. [105] applied *S. cerevisiae* 3 and *H. osmophila* 1056 to improve the quality of ewe's milk and found that both strains provided promising kinetic parameters and improved flavor. They generated a variety of organic acids and could be inoculated with bacterial starters to create products with higher varieties of flavor compounds. Additionally, they acted as biocontrol agents against some mycotoxigenic molds. In a study by Chen et al. [174], *S. cerevisiae* and *K. marxianus* isolated from Koumiss were found to produce mycocin. Typically, the mycocin extracts from *K. marxianus* yeast showed stable and effective antibacterial properties against pathogenic *Escherichia coli* both in *vivo* and in *vitro*, suggesting its potential use as an *E. coli* growth inhibitor. Yeasts from fermented foods and beverages have been reported to secrete various substances, including volatile acids, killer toxins, organic acids, antibiotic factors, and other compounds. Furthermore, *K. marxianus* was found to improve the nutritional value and sensory characteristics of goat milk [226]. These findings suggest that *K. marxianus* has potential as a probiotic strain for use in fermented milk products.

4. Commercial application

The use of yeast as a biocontrol agent in postharvest disease management holds great potential due to its effectiveness, safety, and sustainability. However, despite the extensive research conducted on yeasts as biocontrol agents, commercialization of yeast-based biocontrol products in the processed food industry has been limited. The stark contrast between the numerous "biocontrol yeasts" extensively documented in scientific literature and the limited number of yeast-based protection products officially registered and available in the market is notable. Various factors, such as a deficiency in mechanistic understanding, challenges and expenses associated with product registration, a scarcity of partnerships or consortia with the necessary expertise, and perceived limited commercial potential, likely contribute to the apparent challenges in the development of yeast-based plant protection products [162]. Nonetheless, ongoing research efforts in this area aim to develop consistent and reliable yeast-based biocontrol products, which have the potential to contribute significantly to the reduction of postharvest food losses and enhance food safety.

Few companies offer antagonistic yeasts including IRTA (Sipcam-Inagra, Spain), Bio-ferm (Austria), Koppert (The Netherlands), IOC (France) and ICV (Lalleman). Table 4 listed a few commercially available bioprotective products that have been developed with the aim of controlling diseases both before and after harvest in fruits and vegetables. Several yeast strains here reported, including *C. sake, C. oleophila, A. pullulans, M. fructicola, S. cerevisiae,* have been registered for use on several different fruits. The ability to manage postharvest diseases on different commodities is critical to the economic viability of post-harvest biocontrol products. For

Table 4
Some commercially available bioprotective products developed to control pre- and post-harvest diseases in fruits and vegetables [18,227–229].

Biocontrol Products	Country/Company	Antagonistic yeasts	Fruit	Targeted pathogens
Candifruit™	IRTA/Sipcam-Inagra, Spain	*C. sake*	Pome	*Penicillium, Botrytis, Rhizopus*
Aspire™	United States	*C. oleophila*	Citrus fruits, pome fruits, apple, peach	*P. expansum* *B. cinerea* *R. stolonifer*
Nexy™	France	*C. oleophila*	Pome fruits, citrus, banana	*B. cinerea,* *P. expansum*
Blossom Protect™	Bio-ferm, Austria	*A. pullulans*	Pome	*Penicillium, Botrytis, Monilinia*
YieldPlus™	Canada	*C. albidus*	Citrus, pear, apple, pome fruits	*Botrytis* spp., *Penicillium* spp., *Mucor* spp.
BoniProtect® Botector®	Bio-ferm, Austria	*A. pullulans* (2 strains)	Pome Fruit Grape	*Penicillium, Botrytis, Monilinia*
Noli™	Koppert, The Netherlands	*M. fructicola*	Table grape, Pome fruit, Strawberry, stone Fruit, sweet Potato	*Botrytis, Penicillium, Rhizopus, Aspergillus*
Shemer™	The Netherlands	*M. fructicola*	Grape, carrot strawberry, sweet potatoes, pepper, citrus, apricot, peach	*A. niger, B. cinerea, P. digitatum, P. italicum, R. stolonifer*
Romeo™	France	*S. cerevisiae* (cell walls)	Lettuce, tomato, strawberry, cucumber, grapevines	*B. cinerea* *Erysiphales*
Gaia™	IOC, France	*M. fructicola*	Harvested grape, withering grape, grape musts	*Botrytis,* non-*Saccharomyces* spoiling yeasts
Nymphea™	ICV/Lallemand, France	*Torulaspora delbrueckii*	Harvested grape, grape musts	*Botrytis,* non-*Saccharomyces* spoiling yeasts

example, *C. oleophila* is the first yeast to be developed as a commercial plant protection agent. Its antagonism against *P. digitatum, B. cinerea* and *Alternaria alternata* have been highlighted when applied to grape, citrus, apple, and kiwifruit [39,81,134]. Shemer, based on *M. fructicola*, has demonstrated successful application to various fruits and vegetables, both pre- and post-harvest against *A. niger, B. cinerea, P. digitatum, P. italicum,* and *R. stolonifera.* Additionally, the biocontrol product BoniProtect™ (*A. pullulans*) is advised for pre-harvest application to inhibit the development of wound pathogens such as *P. expansum*, *B. cinerea*, and *Monilinia fructigena* [18].

Alternative plant protection solutions, such as bioprotective yeasts, will certainly be promoted by the general trend of reducing pesticide use. To boost commercial use of antagonistic yeasts for pre- and post-harvest fruit, priority is given to biosafety validation, exploring mechanisms of action, optimizing commercial biological controls, developing multifunctional antifungal products, extending shelf-life, managing costs, and understanding the complex interactions in biological control systems. This integrated approach is critical for practical applications in the fruit and food industry.

5. Application limitations and future recommendations

Yeasts have a long history of use in food and beverage production and are also consumed as food supplements. Many yeasts used in the food industry, such as *S. cerevisiae*, *C. sake*, and *M. pulcherrima*, are closely related to those used in biocontrol. While the use of yeasts as biocontrol agents in food production is generally considered safe, it is important to recognize that certain yeast species, such as some strains from *Pichia* spp. and *Candida* spp., can still pose a risk to human health [230]. These opportunistic yeasts can cause infections in humans under certain conditions, and more research is needed to better understand their pathogenic and virulence factors. Additionally, it is important to monitor whether the increased use of biopreservative yeasts will lead to an increase in the prevalence of yeast infections in humans. While yeasts are not commonly reported to occur as plant pathogens, there have been some cases where they have been found to be pathogenic to certain plants. For example, Giobbe et al. [144] reported that a strain of *P. fermentans*, which was effective in controlling *Monilinia* brown rot when added to apple, was found to be pathogenic to peach, causing rapid decay of fruit tissues. The production of bioactive or allergenic metabolites is another potential concern associated with the use of antagonistic yeasts in the food industry. The use of biocontrol agents may help reduce the usage of chemical preservatives in food products. Moreover, a better understanding of the pathogenicity and virulence factors of opportunistic yeasts could facilitate the development of new yeast-based products. The use of biocontrol agents in the food industry as a component of an integrated approach of biocontrol and bioprotection is expected to gain increasing recognition and be more widely accepted in the coming years. However, safety concerns associated with opportunistic yeasts and potential production of bioactive or allergenic metabolites should be carefully evaluated.

Data availability statement

Datasets published in the literature.

CRediT authorship contribution statement

Yan He: Writing – original draft, Investigation, Conceptualization. **Pascal Degraeve:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Nadia Oulahal:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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